

A SEX-AGE, DENSITY-DEPENDENT MATRIX MODEL FOR WHITE-TAILED DEER POPULATIONS INCORPORATING ANNUAL HARVEST

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ABSTRACT. We model white-tailed deer population by an age and sex structured matrix model based on the discrete-time form of the logistic equation and the Leslie matrix model. Our model adds structure to Jensen's 1995 model for density-dependent population growth, by allowing for different harvest rates based on the age of the deer. We examine the impact of three harvest strategies: collecting both males and females, collecting females only, and collecting males only.

1. MATRIX MODELS

1.1. Leslie matrices. A major subfield of mathematical biology is population dynamics, in which a central goal is to determine how the population of a species changes as time passes. This problem can be refined by dividing the population of a species into groups, and modeling the change in the population of each group as time passes. Such a model is called a *structured model* for population dynamics. For example, if we let $N_{x,t}$ be the number of females of a certain species whose age is between x and $x + 1$ living at time t , then the vector $\vec{N}_t = (N_{0,t}, N_{1,t}, N_{2,t}, \dots)$ recording the species' population is called the *age distribution* (of females) at time t .

One way to determine the age distribution of a population at a future time is to use a Leslie matrix model [L1]. A basic Leslie matrix calculates what happens to each specific age group of females over time, using fixed natality and mortality rates for each age group. (In Leslie's original work, females are only distinguished by whether or not they are at or above age for sexual maturity.) In a Leslie model, we assume

$$(1) \quad \vec{N}_{t+1} = M\vec{N}_t$$

where M is a matrix called a *Leslie matrix*. In particular¹,

$$M = \begin{pmatrix} F_0 & F_1 & F_2 & \dots & F_m \\ P_0 & & & & \\ & P_1 & & & \\ & & \ddots & & \\ & & & P_{m-1} & \end{pmatrix}$$

where P_x is the probability that a female whose age is between x and $x + 1$ will survive another time interval to time $t + 1$ (thus becoming a female of age between

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¹Throughout this paper, blank entries in any matrix are zero.

$x + 1$ and $x + 2$), and F_x is the number of daughters born between time t and $t + 1$ from mothers whose age is in the interval $[x, x + 1)$.

To estimate the long-term age distribution using a Leslie matrix model, one can iterate equation (1) repeatedly to estimate the steady state (i.e. a vector N such that $\approx M^n \vec{N}$ for large n). This has been done in several contexts [L1], [L2], [Lew].

1.2. Density-dependent matrix models. One problem with a Leslie matrix model is that it neglects decline in fecundity as the population density of a species increases [ACG]. Density-dependent effects, such as fecundity rates, keep populations from growing exponentially [ACG], and Leslie matrix models are not complicated enough to account for these effects [J2].

By analogy, if there is only one caste in the population, then a Leslie matrix model corresponds to the exponential growth equation $N_{t+1} = rN_t$; to incorporate density-dependent effects in this setting one might use a logistic model ($N_{t+1} = N_t + \frac{K-N_t}{K}rN_t$). In 1995, Jensen [J2] created a matrix version of the discrete-time logistic equation to describe population change over time. This equation is designed to improve a Leslie model by accounting for density-dependent effects. Jensen's model is as follows:

$$(2) \quad \vec{N}_{t+1} = \vec{N}_t + D(N_t)(M - I)\vec{N}_t.$$

Here, M is the original Leslie matrix, I is the identity, and $D(N_t)$ is a function which models the density-dependent effects. A simple density-dependent function is $D(N_t) = (K - N)/K = (1 - N/K)$, where K is the carrying capacity of the habitat and N is the sum of all values in the vector \vec{N}_t ; this function effectively simulates population change when the initial population size is well below the carrying capacity [J2]. In our models, we set the carrying capacity K to be 1, so that N_t measures the age distribution at time t in terms of percentages of the carrying capacity rather than as raw population counts.

1.3. A sex-age matrix model. To study population dynamics with matrix models, one can divide the population into groups which depend not only on age, but on sex as well. Rather than using \vec{N}_t to represent an age distribution, we now use \vec{N}_t to represent a *sex-age distribution*:

$$\vec{N}_t = \left(\vec{N}_{0,m}, \vec{N}_{0,f}, \vec{N}_{1,m}, \vec{N}_{1,f} \right)$$

where $N_{x,g}$ is the population of age x to $x + 1$ whose sex is g . In this setting, the above equation (2) gives a sex-age matrix model for population dynamics.

1.4. Introducing harvesting. To consider removal of population, Jensen [J1] added additional detail to his 1993 model to account for the removal of some of the population by harvest. Suppose that one is studying population dynamics using a structured model. Also, suppose that one assumes that proportion h_i of the i^{th} caste of the population is removed by harvest per time interval. Then, we define the corresponding *harvest matrix* to be

$$H = \begin{pmatrix} h_1 & & & \\ & h_2 & & \\ & & \ddots & \\ & & & h_d \end{pmatrix},$$

and the *harvest yield* is given by

$$\vec{Y}_t = H\vec{N}_t.$$

The population dynamics are then modeled as follows [J1]:

$$\vec{N}_{t+1} = \vec{N}_t + D(N_t)(M - I)\vec{N}_t - H\vec{N}_t$$

In 2000, Jensen used this model, with sex-age structuring, to simulate the population dynamics of white-tailed deer, assuming for simplicity that the harvest rates $h_{x,g}$ were constant across all age groups. Jensen considered three situations:

- (1) both males and females are harvested at the same rate;
- (2) only males are harvested; and
- (3) only females are harvested.

However, hunters are unlikely to be as interested in harvesting the same number of juvenile deer as older deer. Thus, in this paper we adapt Jensen's model to consider age-structured (as well as gender-structured) harvest.

2. DEER

White-tailed deer (*Odocoileus virginianus*) populations are strongly affected during hunting season harvest. Without annual harvesting, white-tailed deer become overabundant in their habitat [D]. Creating a population dynamics model and studying its long term behavior help us understand how choices of harvest rate affect deer population and harvest yield. In particular, wildlife management groups could use this data by regulating hunting to achieve desired results.

To use a structured matrix model to simulate future population, we need an initial sex-age distribution; it is natural to use an estimate of deer population structure in the absence of hunting for this initial distribution. For white-tailed deer, such data has been obtained by counting deer population in the George Reserve, an area near the University of Michigan with no human activity [J1]. Using data collected from the George Reserve by McCullough [M], Jensen [J1] estimated the sex-age structure in its (harvest-free) "steady-state". This population distribution is given in Table 1 below :

TABLE 1. Projected age structure of deer population at carrying capacity with no harvest [J1]

Age	Total	Males	Females
0	52	26	26
1	50	25	25
2	30	15	15
3	22	11	11
4	16	8	8
5	12	6	6
6	8	4	4
7	6	3	3
*8	4	2	2

The harvest yield is then $\vec{Y}_t = H\vec{N}_t$, and the total yield from the harvest is

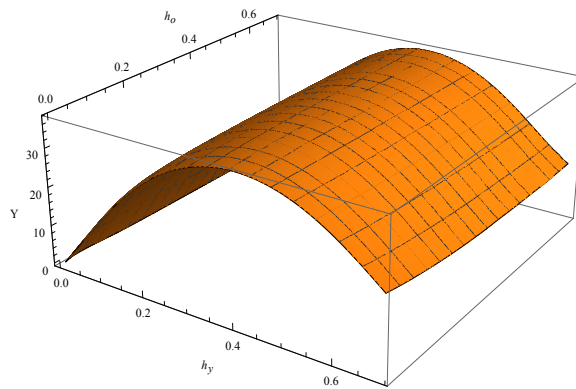
$$Y_t = \sum_{x,g} Y_{t,x,g}$$

4. RESULTS

For each h_y and $h_o \in \{0, .01, .02, \dots, .7\}$, we iterate equation (2) 200 times to find its steady-state, then compute the total yield for that steady-state. We then use 3D graphs to visualise the results. The young deer harvest rate h_y is represented on each graph by the x -axis, and the old deer harvest rate h_o is represented by the y -axis. The z -axis represents the total yield in the steady-state.

4.1. Male and female harvest. Results when both males and females are harvested are given below.

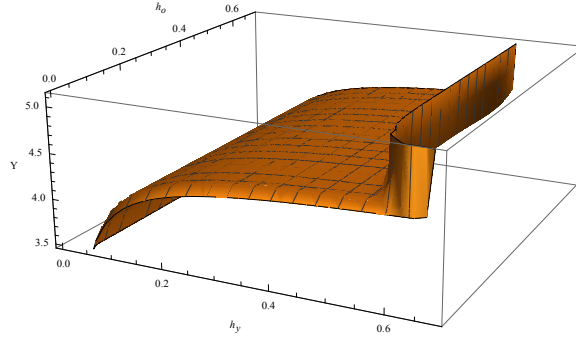
FIGURE 1. Results for harvest of both sexes.



The graph is a concave down surface, with h_y being the main factor in affecting total yield. The yield is optimized when $h_y \approx 37$ percent and when h_o is large, resulting in a total annual yield of 18.73 percent of available deer. If too few or too many young deer are harvested, the total yield decreases significantly. However, h_o has minimal effect on eventual yield.

4.2. Male only harvest. Results of the male harvest are given below. In our model, we simulate male only harvest by setting the h_{yf} and h_{of} parameters to 0.01 to account for accidental harvest of females and to follow Jensen's model [J1].

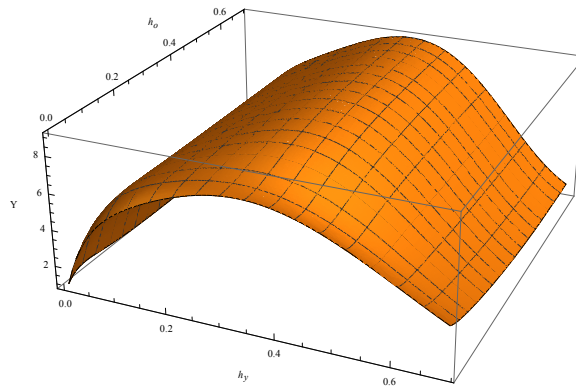
FIGURE 2. Results for harvest of males only.



The graph is slightly concave down when h_y ranges from 0 to 50 percent, but the graph jumps in harvest yield and continues to increase along a nearly linear path for larger values of h_y . Again, h_o has little effect on the eventual yield. The eventual yield has no true maximum, but the eventual yield from male only harvest is nowhere near the yield of harvesting both males and females.

4.3. Female only harvest. Results when only the females are harvested are given below. Similarly to the male only harvest, we set the male harvest parameters, $h_{y,m}$ and $h_{o,m}$, to 0.01. Harvesting females only is considered unorthodox due to their lack of antlers for sport hunters. However, this harvest practice holds interesting mathematical results.

FIGURE 3. Results for harvest of females only.



The graph shows a concave down surface. The maximum annual yield of 4.25 percent of available deer occurs when $h_y \approx 36$ percent and when h_o is large.

4.4. Summary. Total yield is significantly higher when both males and females are collected rather than just males. When harvesting both males and females, our model yields a 1.23 percent increase in total deer harvest over Jensen's model [J1]. However, our model yields a 1.75 percent decrease in female harvests from Jensen. These differences in eventual yield are negligible, since our model so closely relates to Jensen's. However, our model helps us understand that it is the young deer harvest that drives both models. However, the increased maximum yield for male and female harvest may make our model of interest to hunting groups.

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